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The strand flora of the Hawaiian Archipelago—I. Geographical relations, origin, and composition

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GEOGRAPHICAL RELATIONS

For a long time botanists have manifested particular interest in the strand vegetation of various countries. The floras of many continental and insular strands have alike yielded significant material. There is, however, absolutely no comprehensive account of the Hawaiian littoral. Fragmentary and uncoördinated notes concerning various Hawaiian strand plants are given by Hillebrand, Wawra, Gray, Chamisso, Heller, Mann, Schauinsland, Forbes, and other botanists, who at various times during the past century have studied the Hawaiian flora. In the works of none of these investigators is the littoral flora given any special prominence or consideration. This is somewhat surprising, as much of the Hawaiian coast line is readily accessible by boat or trail, whereas the montane districts present innumerable difficulties to the explorer and collector.

Guppy ('06),* in connection with his suggestive studies of plant dispersal in the Pacific, visited the Hawaiian Archipelago and studied the strand flora with reference to the general problems of evolution and distribution. Frequent references are made to Guppy's work in the present paper. His brilliant theories will undoubtedly require more or less revision as data concerning the Pacific flora become more comprehensive and standardized.

* The literature cited will be listed in the second paper of this series.

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The unique position of the Hawaiian Islands, as the most northern group of the great Polynesian island series, and as a region of extreme isolation, gives *particular significance* to its strand flora. The absences from this flora are as important criteria as are the species actually present, and in many ways contribute as effectively to our knowledge of the origin and history of Hawaii's strand flora.

The attempt is here made to present a salient account of the Hawaiian littoral flora, both from the standpoint of content and dispersal, and also from the ecological viewpoint. In the latter phases of the subject the author has been particularly interested. During a residence of nine years in the islands he has made hundreds of excursions along Hawaiian strands, including the principal islands of the archipelago. The present papers incorporate the important data of these field studies.

A noteworthy feature of the littoral floras of the tropical Pacific islands is their *remarkable similarity*. As Hedley ('15) expresses it: "The same species are repeated from atoll to atoll over enormous distances across the Pacific Ocean. The identity of the vegetation possessed by tiny islets separated by thousands of miles of deepest ocean is very striking, since paradoxically they present a *greater continuity of life range than any continent can show*." Many of the more common Hawaiian littoral plants occur on practically all the islands of the archipelago, along an axis of nearly two thousand miles, whereas the montane species are highly localized.

Just as the interior mountainous districts of a high Pacific island contain the majority of the endemic species, so the strand regions are characterized by a majority of the cosmopolitan or wide-ranging species. Tansley and Fritsch ('05) find two main causes for "the striking uniformity of strand plants through the tropics—first, the great similarity of life conditions prevailing on tropical coasts, and secondly, tropical strand plants are mostly adapted for distribution by ocean currents." These factors will be considered in detail in later sections of this paper.

As will be shown later, the Hawaiian littoral flora comprises many species that occur in other parts of the Pacific, and in many other parts of the world. The mountain flora, on the contrary,

is highly endemic and precinctive, and each island possesses an array of peculiar forms. The Hawaiian Islands therefore obey the general law of the cosmopolitanism of littoral constituents.

The geographic situation of the Hawaiian Islands is unique, and has a very important bearing upon the character of the strand flora. There is no other land area of equal magnitude on the earth that is so far removed from continental land areas. The Hawaiian Islands are the most isolated islands, of their size, in the world, and their flora strikingly and faithfully registers this profound and prolonged isolation. An examination of a map of the North Pacific Ocean will show the nature of this isolation. Using the island of Oahu, which is situated in the eastern part of the archipelago, as a base point, the distances to adjacent land-masses, in terms of nautical miles, to ports specified, are as follows:

San Francisco	2,100	Fiji	2,700
San Diego	2,260	Auckland	3,810
Panama	4,665	Sandakan	4,980
Callao	5,147	Hongkong	4,920
Cape Horn	6,488	Yokohama	3,400
Tahiti	2,440	Vladivostok	4,721
Samoa	2,290	Portland	2,360
		Unalaska	2,106

The isolation is further emphasized by an examination of the deep-sea soundings in the vicinity of the Hawaiian Islands, which show that the islands rise from abyssal depths. The great deeps of the Pacific Ocean, which lie between the Hawaiian Archipelago and the continents, are:

Name of deep	Position with reference to Hawaii	Maximum depth in fathoms	Area in square miles
Murray	Due north	3,540	1,033,000
Supan	Due north		
Maury	Due north		
Renard	Northeast		
Wyman	Northeast		
Tanner	Northeast		
Glover	Northeast		
Agassiz	Northeast		
Bache	Northeast		
Moser	Southeast		
Gray	Southeast		
Belknap	South	3,337	165,000
Campbell	South		
Ammen	Southwest		
Brooke	West	3,429	282,000
Bailey	West	3,432	241,000
Tuscarora	Northwest	4,655	908,000

The isolation of the Hawaiian flora is reflected in the vegetation of the littoral zone by the high proportion of endemic species, 32 out of a total of 110, or 30 per cent. Nine of these belong to endemic genera. This is a remarkable showing, since littoral floras, in all parts of the world, are usually comprised almost wholly of cosmopolitan and non-endemic constituents.

South Pacific equivalents of Hawaii

In the comparisons which are likely to be made of the Hawaiian flora with those of the South Pacific islands it is important to recognize the geologic and topographic status of the various island groups. Guppy ('06, p. 14) makes the following significant observationt:

> The Hawaiian Islands, standing alone in the North Pacific, form a floral region in themselves, a region that is the equivalent not of one group in the South Pacific, such as that of Fiji or of Tahiti, but of the whole area comprising all the groups extending from Fiji to the Paumotu Archipelago.

For the purposes of this paper the islands and continental coasts of the Pacific region may be roughly divided into the following great phyto-geographic provinces, listed clockwise in and around this greatest of marine basins. These provinces are not presented as of equal biological value or range, but merely for purposes of convenience in description.

1. Northeastern Siberia and Alaska: Kamchatka, Korake, Tschuktsche, Aleutian Islands, Alaska, British Columbia, and coastal islands.
2. Pacific Coast of North America: Washington, Oregon, California, and coastal islands.
3. Pacific Coast of Mexico and Central America: Lower California, Mexico, Guatamala, Honduras, Nicaragua, Costa Rica, Panama.
4. Pacific Coast of northern South America: Colombia, Ecuador, Galapagos Islands, Peru, Chile, Juan Fernandez Islands.
5. Pacific Coast of southern South America: Chile and coastal islands; Tierra del Fuego.
6. Australasia: Australia, Tasmania, New Zealand, and adjacent islands.
7. Malaysia: Sumatra, Java, Borneo, and other Sunda Islands; Moluccas, New Guinea, Philippine Islands.
8. Southeastern Asia: China, Hai-nan, Indo-China, Cochin China, Cambodja, Siam, Malay Peninsula.
9. Pacific Coast of Central Asia: Japan, Riu-Kiu Islands, Formosa, and adjacent Asiatic coasts and islands.
10. Melanesia: Bismarck Archipelago, Louisiade, Solomon, Santa Cruz, New Hebrides, and Loyalty Islands, New Caledonia, Fiji, and intervening smaller groups.

11. MIKRONESIA: Mariana, Pelew, Caroline, Marshall, and Gilbert Islands, and intervening islands.
12. POLYNESIA—(*a*) *Nuclear Polynesia:* Samoa, Tonga, Fiji, Tokelau, Ellice Islands, etc.
   (*b*) *Central Polynesia:* Cook, Phoenix, Tubuai, Rokahanga, Tongarewa, Manahiki Islands.
   (*c*) *Southeast Polynesia:* Society, Marquesas, Taumotu, Gambier, Pitcairn, Easter, Ducie Islands, etc.
   (*d*) *Northern Polynesia:* HAWAIIAN ISLANDS.
   (*e*) *Southern Polynesia:* New Zealand and Chatham Islands.
   (*f*) *Polynesian Verge:* scattered islands between Polynesia and Melanesia, such as Ticopia.

EXTENT OF THE HAWAIIAN LITTORAL

The great length of the archipelago gives the littoral zone a much larger significance and extent than if the archipelago consisted of but a few islands situated close together. The Hawaiian littoral, ranging for nearly two thousand miles, contrasts sharply with the compact littoral of such groups as Samoa, Tonga, New Caledonia, Ellice and Phoenix. Other Pacific island groups which are extended over long axes, similar to Hawaii, are the Aleutian, Kurile, Paumotu, Marshall, Caroline, and Solomon Islands.

The Hawaiian strand occupies an island series extending from 18° 54′ to 22° 15′ north latitude, and between 154° 50′ and 160° 30′ of longitude west of Greenwich. This range should greatly increase the mathematical probability of plant dispersal, and in some measure tend to neutralize the powerful isolation-factor. The east-and-west range of the littoral naturally results in a much greater homogeneity of flora than would be the case in an archipelago with a dominant north-and-south axis. In this respect the Hawaiian Islands may be contrasted with such archipelagoes as the Philippines, and the Mariana and Maldive groups.

The great variation in the size and elevation of the several islands markedly influences the extent of the littoral. In general, the low islands have strands that extend further back into the interior than do those of the high islands; the small islands have a larger proportion of strand, relative to their total area, than do the large islands. The small, low coral islets that predominate in the western end of the archipelago are littoral throughout practically all their area; the large, high islands of Maui and Hawaii, at the eastern extremity of the archipelago, have a narrow and closely defined strand.

The following islands have *relatively wide strands:*

1. Ocean, Kure, or Cure Island: circular barrier atoll, 16 miles in circumference; area of lagoon about 38 square miles; several low sand islets in the lagoon; considerable shrubbery and other low vegetation on the largest sand islet, "Green Island."
2. Midway or Brook's Island: circular barrier atoll, 18 miles in circumference; area of lagoon about 40 square miles; several low sand islets in the lagoon; native and introduced vegetation.
3. Pearl and Hermes Reef: irregular, oval barrier atoll, 42 miles in circumference; area of lagoon about 80 square miles; numerous low sand islets in the lagoon, some with grasses and other low vegetation.
4. Lisiansky Island: low, oval isle of coral sand; two miles by three miles; lagoon empty of water; surrounded by reef which extends six or seven miles from isle; vegetation very sparse.
5. Laysan Island: elevated, oval atoll; two miles by a mile and a half; well-developed fringing reef; briny lagoon; abundant scrubby vegetation.
6. French Frigates Shoal: crescentic atoll, with numerous low sand isles, and several high, rocky volcanic isles; area of shoal about 30 square miles; extensive reefs; grasses and low vegetation on sand isles.
7. Small isles along the coasts of Oahu, most of them formerly connected with the island; sparse vegetation: Kihewamoku, Mokuaia; Pulemoku; Kukuihoolua; Mokualai; Mokolii; Kapapa; Ahuolaka; Kekepa; Mokuoloe; Mokolea Mokulua; Kaonikaipu; Mokauea; Mokuoeo; Onini; Moku Umaume; Laulaunui.
8. Small isles along the coasts of Molokai, most of them formerly connected with the island; vegetation sparse or absent: Namoku; Mokapu; Okala; Kuelo-Lepau; Mokuhooniki; Kanaha; Puukole.
9. Small isles along the coasts of Hawaii: Coconut Island, etc.

Narrow strands are characteristic of the following islands:

10. Niihau: area 97 square miles; highest point, 1,300 feet.
11. Kauai: area 547 square miles; highest point, 5,250 feet.
12. Oahu: area 598 square miles; highest point, 4,030 feet.
13. Molokai: area 261 square miles; highest point, 4,958 feet.
14. Maui: area 728 square miles; highest point, 10,032 feet.
15. Lanai: area 139 square miles; highest point, 3,400 feet.
16. Kahoolawe: area 69 square miles; highest point, 1,472 feet.
17. Hawaii: area 4015 square miles; highest point, 13,825 feet.

A number of the smaller islands of the Hawaiian Archipelago rise very abruptly from the sea, and are characterized by *steep or precipitous coasts.* The following are of this type:

18. Gardiner Island: conical rock, 700 feet in diameter, 175 feet high; cliffs 60–70 feet high on all sides; a smaller, precipitous rock nearby.
19. French Frigates Shoal: volcanic rocky islet in center of formerl agoon; 180 feet long, 45 feet wide, 120 feet high; vertical walls; barren.
20. Necker Island: remnant of volcanic crater, surrounded by reef; isle is three quarters of a mile long, 500 feet wide, and 300 feet high; scanty vegetation sea-cliffs on all sides.

21. Nihoa, Bird Island or Moku (Modu) Manu: volcanic remnant; three quarters of a mile long, one third of a mile wide, 600–900 feet high; sea-cliffs on all sides; vegetation scanty.
22. Small isles along the coast of Niihau, probably at one time connected with the island: Kaula and Lehua, small eroded cinder cones with sea-cliffs and steep slopes.
23. Small isles along the coast of Oahu: Moku Manu (two volcanic remnants); Manana (Rabbit Island), eroded crater, with sea-cliffs.
24. Small isles and rocks along the coasts of Molokai: Mokolea, Mokohola, Mokomana.
25. Small isles along the coasts of Maui: Molokini, etc.
26. Five Needles: a group of detached pinnacle rocks about 120 feet high, situated five and a half miles north of Cape Kaea, Lanai, and about the middle of the bight on the west side of the island.

The largest strand areas on any single island occur on the island of Hawaii; the smallest strands are those of the tiny islets in the westward end of the archipelago. On the whole, the Hawaiian strand, as a phytogeographic province, is *poorly developed* when compared with the Indo-Malayan or West Indian strands, or with those of numerous other archipelagoes.

SUBSIDENCE AND ELEVATION

A factor of far-reaching importance in any biological studies in the Hawaiian Archipelago is that of subsidence, i. e., the islands are but the apices of lofty and slowly-sinking submarine mountains. Physiographical evidence is accumulating to show that during previous stages in the history of the central Pacific, these islands undoubtedly stood *thousands of feet higher* than they do at present. Many stages of subsidence and erosion may be found today within the group, ranging from the large, actively volcanic island of Hawaii (nearly 14,000 feet in elevation), at one end of the chain, to the tiny coral atolls, but a few feet above sea-level, which are scattered along the other extremity.

Considering the strand zone of any given island, it is evident that through a long period of time this zone has been slowly *creeping up* the slopes of the island, and the terrestrial vegetation has been crowded into steadily diminishing areas. In other words, the total mileage of strand was formerly much greater than at present, other things being equal. Granting slow subsidence as the prevalent condition of Pacific islands (see, in this connection, an important contribution by Bryan, '16), the great strand mileage

of an island like Hawaii steadily decreases until ultimately the condition exhibited by the tiny strand of Laysan or Midway is reached. In this manner the subsidence-factor, although not of especial force at any one time, has been through long periods of time a powerful influence on the strand flora.

Although subsidence has been the dominant note in Hawaii's geological history, there have been minor elevations within recent times. Raised coral reefs and beaches occur at various points along the coasts, e. g., along the southern and western shores of Oahu. The highest reef known is on the southwestern end of Mailiilii, elevated 120 feet above the sea. Just as local elevation at such points as Mokapu, Kalihi, and the Coral Plain has pushed the littoral zone seaward, so at Hanalei, Kahana, Kaneohe, and Pearl Harbor the drowning or submergence of valley-mouths has developed deep embayments, and the littoral flora extends deep into the lowland zone which surrounds it on three sides. It is evident that sufficient study and emphasis has not been given to the ecological effects of these gradual changes of land- and sea-level.

In his illuminating studies of the New Zealand flora, Aston ('12) concludes that the raised marine beaches at Cape Turakirae show that there has occurred comparatively recently, and perhaps within historic times, rapid elevation of the coast line. Violent earthquakes have so altered the physiography of the littoral as to result in some unusual ecological features.

ORIGIN

Relation of Pacific Ocean currents to the dissemination of plants of the Hawaiian littoral

The importance of ocean currents as agencies for the distribution of plants, and more particularly for the wide dissemination of beach species, has long been recognized. In a vast body of water, like the Pacific, dotted with thousands of scattered islands, the surface currents assume special significance in relation to the migrations of plants, animals, and man.

The surface circulation of the Pacific is, on the whole, notably less active than that of the Atlantic. The vertices of the rotational movements are marked by "Sargasso Seas" in the north and

south basins, but these quiet areas are of small extent when compared with the well-known Sargasso Sea of the North Atlantic Ocean.

Reference should here be made to the Northern Equatorial Current, which receives important contributions from the great stream that sweeps down the North Pacific coast of America. Many of the largest and most famous of the Hawaiian double canoes were hewn from Douglas spruce (*Pseudotsuga taxifolia*) which had been carried to the shores of Niihau, Kauai, and other islands by the currents. It is a well-known fact that the natives of the Alaska islands obtain much of their fire-wood as drift from the Asiatic coast. Japanese fishing-boats, at various times in history, have drifted to the Hawaiian Islands and to the northwest coast of America.

Between the two great equatorial currents flowing westward on either side of the equator there is a narrow counter-equatorial current flowing to the east. This stream is largely assisted during the latter half of the year by the southwest monsoon, and from July to October the southwest winds prevailing east of 150° E. further strengthen the current, but later in the year the easterly winds weaken or even destroy it. The currents of the South Pacific are well shown in Schimper's ('91) monograph of the Indo-Malayan strand flora.

A feature of ocean currents as seed carriers that has not been sufficiently emphasized is the definiteness of their courses. This fact is well illustrated by the large number of tree trunks and logs from the North Pacific coast that are annually cast upon the Hawaiian coasts. These trees occur in a relatively small and well-defined region, and evidently follow a definite course across the North Pacific. Wood-Jones ('12) performed an interesting experiment to determine the course of drift material in the Indian Ocean. He cast adrift, in the Cocos-Keeling Islands, bottles containing messages. One was picked up on the beach of Brava, Italian Somaliland, after a journey of three thousand miles across the Indian Ocean, and a second one, sent out nearly a year later, was washed ashore at precisely the same place. This definiteness of course gives to the ocean currents a high potential cumulative effect as carriers, that merits more than passing mention.

Currents in the vicinity of Hawaii

The United States Coast Pilot contains data concerning the local island currents, which may be summarized as follows. The strong northeast trades begin early in March, blowing well from the northward until May, and from then until October they are more easterly. During October the trades are light with frequent calms, and occasionally a west southwest swell sets in. During November and December the trades are strong and variable, occasionally being interruped by light southerly winds. During January and February southerly and southwesterly gales often prevail. These are *konas* and are from a few hours to two or three days duration, followed by rain.

Hawaii.—Generally the currents follow the trades but occasionally they set against the wind. A current follows the coast north of Cape Kumukahi around Upolu Point; another one follows the trend of the coast offshore southwestward from Cape Kumukahi around Kalae and northward as far as Upolu Point. There is an inshore current that sets southward from Okoe Landing along the west coast around Kalae, and thence northeastward along the shore as far as Keauhou.

Maui.—Generally the currents set with the trades. A current follows the north shore of Maui westward from Kauiki Head and draws down through Pailolo Channel; the current is stronger on the Molokai side of the channel. A strong current follows the coast southward of Kauiki Head until past Kahoolawe. In the vicinity of Lahaina the current generally sets northwestward.

Molokai.—The current sets westward along the entire northerly coast, and about half the length of the southerly shore, where an easterly current prevails.

Oahu.—The currents around Oahu are variable in strength and direction, but the general movement of the water along the coast is westward or northwestward, the direction being modified by the trend of the coast.

Kauai.—Currents are very uncertain as to direction but they generally follow the winds, though frequently setting in the opposite direction during the first calms after strong trades.

A careful study of any good map which depicts the ocean cur-

rents of the North Pacific Ocean will graphically show that the Hawaiian Archipelago is practically outside the zone of influence of the great currents that would naturally bring the seeds of tropical plants to her shores. Guppy's statements ('06, pp. 75, 64) are pertinent in this connection:

> The currents of the Pacific have failed to establish the numerous beach-trees (possessing buoyant fruits) of the Pacific Islands, not only in the Hawaiian group, but also on the coast of America; and it is therefore argued that we should expect the Hawaiian group to have received through the currents its shore-plants with buoyant seeds or fruits from the tropical west coasts of America.
>
> In support of this contention it is pointed out that most of the Hawaiian strand-plants that are dispersed by the currents are found in America, and some indeed in America to the exclusion of the Old World.
>
> The arrangement of the currents in the North Pacific also favours the view that the Hawaiian Islands are more likely to receive plants by the agency of the currents from America than from the Asiatic side of the Pacific.
>
> . . . .
>
> Speaking generally of the extension eastward of the Indo-Malayan strand-plants over the Pacific, Professor Schimper (['91] page 195) remarks that they become fewer and fewer in number as they extend farther from their original home, their number shrinking to a very few in the most remote groups of the Marquesas and the Hawaiian Islands. . . . The number actually introduced through the currents into Hawaii in all likelihood, therefore, does not exceed ten.

Importance of drift material

Drift material is much more abundant along the Hawaiian windward shores than on the leeward shores. Nowhere does it attain the proportions that characterize many other regions elsewhere on the globe. Certain districts, for example, the southeast coast of Hawaii, between Honuapo and Kalae, particularly the Kamilo beach near Kaluwalu, seem to be much more favorably situated for the reception and accumulation of drift than do others.

Tansley and Fritsch ('05) describe the abundant drift on portions of the Ceylon littoral, and note the great variety of plant fragments, fruits, and seeds:

> The thickest masses of drift were very moist and quite warm to the hand, and in this natural forcing bed many different plants had germinated. The thick line of brown-black humus with the fresh green leaves of the seedlings arising from it at intervals was a most striking sight. Of these the most conspicuous were *Cerbera odollam*, *Calophyllum inophyllum*, *Bruguiera gymnorhiza*, *Crinum asiaticum*, and *Colocasia antiquorum* (from bits of old rhizome).

Moseley ('79, p. 367) reports from the Moluccas living epiphytic

orchids and young palms as part of the drift, washed high up on the beach and growing. He states:

> We passed large quantities of leaves, fruits, and flowers, and branches of trees floated off from the shores. . . . I was astonished at the large quantities of fresh vegetable matter thus seen floating on the sea. . . . Not only are large quantities of fruits [containing seeds] capable of germinating thus transported from island to island, but entire living plants, even trees, are washed from island to island and transplanted by the waves.

Hooker ('47, p. 253) states that the majority of the littoral species of the Galapagos Islands have reached the islands through oceanic and aerial currents. There are about twenty such plants, mostly species common to warm latitudes. Some of these are: *Cissampelos Pariera*, *Tribulus cistoides*, *Tephrosia littoralis*, *Verbena littoralis*, *Avicennia tomentosa*, *Scaevola Plumieri*, *Ipomoea maritima*, *Calystegia Soldanella*, and *Heliotropium curassavicum*. Hooker attributes the following plants of the Peruvian and Chilean littoral, which occur on the Galapagos strand, to ocean currents: *Vigna oahuensis*, *Acacia Cavenia*, *Nicotiana glutinosa*, *Dictyocalyx Miersii*, *Lycopersicum peruvianum*, *Verbena littoralis*, *V. polystacha*, and *Plantago tomentosa*.

Flotation adaptations of strand plant seeds

In his monograph on the Indo-Malayan strand flora Schimper ('91, pp. 163–178) makes the following classification of strand plants, based upon the flotation characters:

1. Driftfrüchte und Driftsamen mit grossen luftführenden Hohlräumen. Examples: fruits of *Heritiera littoralis*, *Thespesia populnea*, *Pongamia glabra*, and *Derris uliginosa;* seeds of *Mucuna* species, *Caesalpinia Bonducella*, *Vigna lutea*, *Hibiscus tiliaceus*, *Dodonea viscosa*, *Euphorbia Atoto*, *Suriana maritima*, *Ipomoea pes caprae*, *Pangium edule* (?), *Colubrina asiatica* (?), *Morinda citrifolia*.
2. Driftsamen mit schwammigen Samenkern. Examples: many Leguminosae, such as *Sophora tomentosa* and species of *Erythrina* and *Canavalia;* embryos of *Rhizophora* and *Avicennia*.
3. Driftfrüchte und Driftsamen, deren Schwimmfähigkeit durch luftführendes Schalengewebe bedingt ist.
   - A. Schwimmgewebe peripherisch. Examples: *Clerodendron inerme*, *Carapa* species, *Cordia subcordata*, *Wollastonia glabra*, *Tournefortia argentea*, *Pemphis acidula*.
     - a. Schwimmgewebe mit grossen Intercellularräumen. Examples: *Cerbera Odollam*, *Laguncularia racemosa*, *Nipa fruticans*.
     - b. Schwimmgewege ohne oder nur mit winzigen Intercellularräumen. Examples: fruits of *Cocos nucifera*, *Barringtonia speciosa*, *B. excelsa*, *Ter-*

minalia Katappa, Conocarpus erecta, Lumnitzera racemosa, L. coccinea, Scyphiphora hydrophyllacea, Guettarda speciosa, Tournefortia argentea, Wollastonia glabra, Scaevola Koenigii, Clerodendron inerme, Cynometra cauliflora, Cordia subcordata; seeds of *Carapa moluccensis, C. obovata, Sonneratia* species, *Pemphis acidula.*

B. Das Schwimmgewebe befindet sich innerhalb einer harten Stein- oder Samenschale. Examples: fruits of *Calophyllum inophyllum* and *Ximemia americana;* seeds of *Cyas circinalis* and *Excoecaria Agallocha.*

Guppy ('06, p. 531) enumerates the following seeds or seed vessels that remained afloat after a year's flotation in sea-water: *Thespesia populnea, Mucuna gigantea, Dioclea* sp., *Strongylodon lucidum, Sophora tomentosa, Caesalpina Bonducella, Entada scandens, Morinda citrifolia, Scaevola Koenigii, Cordia subcordata, Tournefortia argentea, Ipomoea grandiflora,* and *Tacca pinnatifida.*

In Helmsley's classification of the Bermudian flowering plants ('85, p. 48) the following indigenous genera, chiefly littoral forms, are listed as having probably been conveyed to the island by ocean currents: *Cakile, Hibiscus, Suriana, Elaeodendron, Sapindus, Dodonaea, Cardiospermum, Rhus, Sophora, Vigna, Canavalia, Centrosema, Conocarpus, Rhizophora, Opuntia, Sesuvium, Rhachicallis, Chiococca, Morinda, Solidago, Borrichia, Scaevola, Tournefortia, Heliotropium, Ipomoea, Convolvulus, Avicennia, Coccoloba, Atriplex, Salicornia, Euphorbia, Croton, Ruppia, Zostera, Cenchrus, Spartina, Stenotaphrum, Sporobolus, Chloris.*

Helmsley ('84, p. 304) has also recorded the actual germination of various drifted seeds after being cast ashore. He lists *Hibiscus tiliaceus, Vitis vinifera, Sapindus Saponaria, Anacardium occidentale, Aleurites moluccana, Ricinus communis, Cocos nucifera,* and *Sagus* sp. Of *Vitis vinifera* he records the foundering of a vessel laden with a cargo of white Lisbon grapes, off the south shore of Bermuda. Many of the grapes were washed ashore, and the seeds germinated at high-water mark. Numbers of plants were taken up, out of curiosity, and transplanted, and bore fruit. Martins raised plants from seeds of *Ricinus communis* that had been floating for ninety-three days upon the surface of the sea.

Shull's ('14) extensive experiments show that the seeds of many species will germinate after four years of continuous submergence in fresh water, and that the seeds of three species were viable after seven years of continuous submergence.

Guppy ('06, p. 529) shows that of the littoral plants of Fiji and Tahiti, 75–80 per cent. have seeds or fruits that will float unharmed for two months or more, and that about 30 per cent. of this number are legumes. He says:

> In the course of the ages the plants with buoyant seeds or seed vessels have been gathered at the coast. This is indicated: (1) By the far greater proportion of species with buoyant seeds and seed vessels amongst the shore plants than among the inland plants. (2) By the circumstance that almost all the seeds or seed vessels that float unharmed for long periods belong to shore plants. (3) By the fact that when a genus has both inland and littoral species, the seeds or fruits of the coast species as a rule float for a long time, while those of the inland species either sink at once or float only for a short period.

Guppy ('06, p. 563) makes the following list of "Hawaiian plants with buoyant seeds and fruits known to be dispersed by the currents either exclusively or, as in a few species, with the assistance of frugivorous birds": *Colubrina asiatica*, *Dioclea violacea*, *Mucuna gigantea*, *M. urens*, *Strongylodon lucidum*, *Vigna lutea*, *Caesalpinia Bonducella*, *Scaevola Koenigii*, *Ipomoea glaberrima*, *I. Pes-caprae*, *Vitex trifolia* and *Cassytha filiformis*. Although many strand plants possess seeds or fruits that can float for long periods, other widely distributed species possess feeble or no flotation power. It is necessary to recognize other agencies.

Trees and logs as disseminators

Logs and tree-trunks of various coniferous species from the Puget Sound region are commonly cast ashore upon the Hawaiian windward coasts. It is a matter of common observation that on all windy coasts, small seeds, like sand, are blown into every available cranny. In this way many lodge in the holes and cracks in drift-wood, which is floated off at high tide or during storm time, and thus the seeds or fruits may be carried to new localities. Strand seeds or fruits which do not possess special flotation devices may be carried to new shores. Moreover, the seeds of inland species may be carried by trees which have been uprooted by inundations or storms, either in the soil around the roots, or in the bark, etc.

Ernst ('08, p. 56) states that "tree stems and branches played an important part in the colonization of Krakatau by plants and animals." Hedley ('15) records a log of *Dammara australis*

the New Zealand Kauri, as stranding on the windward reef of Funafuti. Wood-Jones ('05) gives an excellent account of tree-trunks and "floating islands" of storm-washed vegetation as carriers of seeds, animals, etc., to the Cocos-Keeling group. He emphasizes the importance of trees with buttressed bases as disseminators:

> These buttresses are in the form of large thin wings, which taper to the trunk above, and below form a series of compartments like stalls in a circular stable. Within these stalls much earth is held fast by the interlacing of smaller roots, and when such a tree is uprooted, and set adrift to sea, it carries its earth with it. It may carry it for very great distances, and I have seen a buttressed tree come ashore in the atoll, from whose base a wheelbarrow-load of fine red earth might have been collected.

FLOATING ROCKS AS DISSEMINATORS

The idea of floating rocks as disseminators of littoral plants might be met with incredulity, were it not for the testimony of many reliable observers. Among the volcanic islands of the East Indies large blocks of pumice float for many weeks, and are carried many hundred miles from their points of origin. The salient points—prolonged flotation of the blocks; presence of numerous kinds of seeds in the crevices and pores of the pumice; and the germination of these seeds when the block is cast upon a favorable beach-situation—have all been corroborated by careful investigators. Ernst ('08, p. 56) states that floating blocks of pumice constitute an important dispersal agency in the Sunda-Straits region.

Although there is very little pumice to be found on the Hawaiian coasts at the present time, there is abundant evidence that in earlier periods in the geologic history of the islands, repeated volcanic explosions, resulting in pumice production, have taken place. There are today extensive pumice beds around the volcano Kilauea. Therefore, although pumice blocks play little or no part in the dispersal of plants in the Hawaiian group at present, it is entirely possible that they had a more important rôle in earlier times, at least in distributing seed from island to island.

Floating masses of dead coral may also be ranked as possible seed-carriers. Wood-Jones ('15) found numerous instances of this in the Cocos-Keeling group. The innumerable air-cavities in certain kinds of coral render it buoyant. The block is cast upon a beach at storm time; it lies there for an indefinite period;

earth, sand, and seeds lodge in its many crevices; another storm sets it again adrift; and it may be cast ashore upon a distant strand. Coral blocks of this sort are infrequent on Hawaiian shores, owing to the relative paucity of fringing reef, and have probably been of minor significance in seed dispersal. They constitute, however, a possible factor, particularly on Oahu, Kauai, and the leeward isles.

COMPOSITION—A CLASSIFIED LIST OF THE HAWAIIAN STRAND PLANTS

I. True littorals

Species which occur only or chiefly within the strand zone.

Endemic littorals

Trees and shrubs

There are no endemic trees that are strictly littoral. This is a significant feature of the Hawaiian flora. The shrubs are:

Lycium sandwicense Gray
Nototrichium humile Hillebd.
Santalum Freycinetianum Gaud. var. *littorale* Hillebd.
Phyllostegia variabilis Bitter
Scaevola coriacea Nutt.
Solanum Nelsoni Dun.
S. laysanense Bitter
Wikstroemia Uva-ursi Gray

Herbaceous plants

Achyranthus splendens Mart.
A. splendens var. *rotundata* Hillebd.
Campylotheca molokaiensis Hillebd.
Fimbristylis pycnocephala Hillebd.
Kadua littoralis Hillebd.
Lepidium owaihense Cham. & Schlecht.
Lipochaeta connata (Gaud.) DC. var. *littoralis* Hillebd.
L. integrifolia (Nutt.) Gray
L. succulenta (Hook. & Arn.) DC.
Schiedea globosa Mann
S. Lydgatei Hillebd.
Sporobolus virginicus (L.) Kunth var. *phleoides* Hillebd.
Tetramolopium sp.

2. Indigenous littorals

Trees and shrubs

There are no indigenous trees that are strictly littoral. Shrubs:

Colubrina asiatica (L.) Brongn.
Gossypium tomentosum Nutt.

Heliotropium anomalum Hook. & Arn.
Scaevola Lobelia Murr.
Sesbania tomentosa Hook. & Arn.
Vitex trifolia L.

Herbaceous plants

Argyreia tiliaefolia (Desr.) Wight
Boerhaavia diffusa L.
Cressa cretica L.
Cyperus laevigatus L.
Euphorbia cordata Meyen
Heliotropium curassavicum L.
Herpestis Monnieria H. B. K.
Ipomoea acetosaefolia (Vahl) Roem. & Schl.
I. glaberrima Bojer
I. insularis Steud.
Ipomoea Pes-caprae (L.) Sweet
Lepturus repens R. Br.
Lysimachia spathulata Benth. & Hook.
Ruppia maritima L.
Scirpus maritimus L.
Sesuvium Portulacastrum L.
Sporobolus virginicus (L.) Kunth
Tephrosia piscatoria (Soland.) Pers.

3. LITTORALS INTRODUCED BY THE PRIMITIVE HAWAIIANS*

Trees

Calophyllum Inophyllum L.
Cocos nucifera L.
Cordia subcordata Lam.

4. LITTORALS INTRODUCED SINCE THE ADVENT OF EUROPEANS (1555–1778 TO DATE)

Trees and shrubs

No true littoral trees and shrubs have been introduced.

Herbaceous plants

Batis maritima L.
Polypogon littoralis (With.) Sm.

II. Pseudo-Littorals

Species which chiefly inhabit the lowlands or other zones, and which appear on the strands in the role of invaders from the interior.

1. ENDEMIC PSEUDO-LITTORALS

Trees and shrubs

Acacia koa Gray
Cassia Gaudichaudii Hook & Arn.
Chenopodium sandwicheum Moq.
Erythrina monosperma Gaud.
Myoporum sandwicense (A. DC.) Gray

* *Thespesia populnea* Soland. should be noted here.

Herbaceous plants

Carex sandwicensis Boeckl.
Jacquemontia sandwicensis Gray
Nama sandwicensis Gray
Peucedanum sandwicense Hillebd.
Sicyos hispidus Hillebd.
S. microcarpus Mann

2. Indigenous pseudo-littorals

Trees and shrubs

Caesalpinia Bonducella (L.) Flem.
Metrosideros polymorpha Gaud.
Pritchardia spp.
Tribulus cistoides L.

Herbaceous plants

Argemone mexicana L.
Cassytha filiformis L.
Cenchrus calyculatus (Spreng.) Cav.
Chenopodium album L.
Cladium leptostachyum Nees
Cyperus pennatus Lam.
C. phleoides Nees
Eragrostis hawaiiensis Hillebd.
Erythraea sabaeoides (Griseb.) Gray
Fleurya interrupta Gaud.
Kyllingia monocephala Rottb.
Lythrum maritimum H. B. K.
Malvastrum tricuspidatum (Ait.) Gray
Mucuna gigantea (Willd.) DC.
Ophioglossum vulgatum L.
Sida spp.
Vigna lutea (Sw.) Gray
Waltheria americana L.

3. Pseudo-littorals introduced by primitive Hawaiians

Trees

Aleurites moluccana (L.) Willd.
Hibiscus tiliaceus L.
Morinda citrifolia L.
Pandanus odoratissimus L. f.

4. Pseudo-littorals introduced since the advent of Europeans

Trees and shrubs

Acacia farnesiana Willd.
Casuarina equisetifolia Stickman
Hibiscus Rosa-sinensis L.
Leucaena glauca (Willd.) Benth.
Prosopis juliflora (Sw.) DC.

Herbaceous plants

Abrus precatorius L.	*Euxolus viridis* Moq.
Achyranthus aspera L.	*Hydrocotyle verticillata* Thunb.
Cardiospermum Halicacabum L.	*Indigofera Anil* L.
Crotalaria spp.	*Mesembryanthemum* spp.
Cynodon Dactylon (L.) Pers.	*Portulaca oleracea* L.
Cyperus umbellatus Vahl	*Salvia occidentalis* Sw.
Datura Stramonium L.	*Samanea Saman* (Benth.) Merrill
Euphorbia pilulifera L.	*Xanthium echinatum* Murr.

There are numerous ruderals, in addition to those indicated in the last section, that occur at random on the various beaches.

COLLEGE OF HAWAII, HONOLULU